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EMBRYOLOGY.[1]

Experimental Embryology.—Recent numbers of Roux's Archiv für Entwickelungsmechanik contain numerous additions to our knowledge of the possibilities resident in the early stages of the development of animals, possibilities unsuspected till direct experimental interference made them evident.

T. H. MORGAN of Bryn Maur presents evidence[2] to show that two blastulæ of the sea urchin, Sphærechinus, may fuse together and form one embryo. When eggs are shaken just after fertilization they may loose their membranes and afterwards some of the resulting blastulæ are found to have twice the normal size though otherwise like the usual blastulæ in appearance. Such large blastulæ are stated to arise from the fusion of two common blastulæ.

Notwithstanding this complete fusion the future development of such enlarged blastulæ gives evidence of their dual origin. At the gastrula stage *two* invaginations are formed.

One may be much the greater and the two may not appear at the same time. The two invaginations stand in no fixed relation to one another and may appear in all parts of the compounded blastula.

Later the larva that develops from two fused blastulæ tends to develop two sets of arms and two systems of skeletal rods, but those accompanying the lesser invagination are much reduced in size and less perfect than the rods associated with the main invagination.

A second paper[3] by the same worker records a variation in the cleavage of the above sea urchin when some of the eggs were shaken.

While most of the eggs divide into 2, 4, 8 and 16 cells some were found to divide at once into *three.* These 3 cells are elongated parallel to the planes that produced them. When they next divide they all do so lengthwise, in flat contradiction to "Hertwig's law." These six equal cells lie in a plane at right angles to the two cleavage planes that have produced them.

Such eggs may develop into gastrulæ. They form six small cells or micromeres at one pole of the mass in place of the normal four. The author thinks "a micromere field must have been present in the egg prior to division."

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[1] Edited by E. A. Andrews, Baltimore, Md., to whom abstracts, reviews and preliminary notes may be sent.

[2] Vol. II, pps. 65–70.

[3] Idem, pps. 72–80.

Eggs that have not been shaken sometimes divide at once into four cells.

In both these unusual forms of cleavage the author finds that the three or the four archoplasmic centres present in the egg take unequal numbers of chromosomes. Thus in one case one centre was accompanied by 17, another by 14, another by 33 and the fourth by 0 chromosomes.

That this inequality is greater in the four-fold than in the three-fold division explains, the author suggests, the fact that fewer eggs develop from the four-fold than from the three-fold cleavage.

A third paper[4] gives a detailed account of the partial larvæ obtained when the eggs of Sphærechinus are shaken into fragments. Very minute gastrulæ only $\frac{1}{64}$ part of the volume of a normal gastrula are thought to come from isolated pieces with $\frac{1}{40}$ to $\frac{1}{50}$ the volume of the whole egg.

It is found that the number of cells in such small blastulæ is less than the normal number and roughly proportional to the size of the blastula.

The size of the nuclei, and probably of the cells also, is less in the small blastulæ than in the normal ones.

If one of first two cells of a cleaving egg be isolated it may form a blastula with $\frac{1}{2}$ the normal number of cells. One of the first four cells gives a blastula with $\frac{1}{4}$ the normal number, or with a little more than $\frac{1}{4}$; while one of the first eight cells when isolated produces a blastula with more than $\frac{1}{8}$ the normal number.

Such blastulæ will develop into gastrulæ.

A piece of the wall of a blastula when broken off by shaking may develop into a gastrula.

The little blastulæ formed from fragments of eggs tend to invaginate as many cells as possible up to the normal number for a normal gastrula.

These remarkable numerical relations lead the author to suppose that the reason why isolated cells of later stages in cleavage are not able to develop by themselves lies not in any differentiation of nuclear substance but in the fact that such cells being themselves the results of a series of cleavages cannot produce cells enough for the next stages of development.

MORGAN and DRIESCH publish conjointly[5] their reinvestigation of the remarkable halflarvæ obtained by Chun.

[4] Idem, pps. 81–124.

[5] Idem, pps. 203-226.

Chun's work was done 18 years ago and was, as stated in a letter to Roux ;[6] as follows.

When the first two cells of the eggs of the lobate Ctenophore, *Bolina hydatina* were separated by shaking each developed as a halflarva with four ribs or bands of locomoter appendages instead of the normal eight, two entodermal sacs in place of four and only one tentacle in place of two.

The first cleavage plane coincides with the sagittal plane of the adult and the second with the transverse.

Half-larvæ with 4 ribs, 4 meridional vessels one tentacle and an oblique stomach *may become sexually mature,* developing eggs and sperm under the two subventral meridional vessels!

The missing half is regenerated during the postembryonic metamorphosis.

Driesch and Morgan worked on another Ctenophore, a nontentaculated form, *Beroë ovata* and finding it impossible to employ the shaking method cut the eggs with special scissors.

Isolated cells of the two cell stage develop into blastulæ, gastrulæ and finally into larvæ that are most remarkable in being neither complete nor halflarvæ but larvæ deficient in certain organs.

The cleavage of such an isolated cell is much as it would be if still associated with the other cell in a normal egg : it is a half cleavage as compared with a normal egg. This, however, is not true of the cells that form the ectoderm but only of the peculiar group of cells forming the entoderm. The former cells grow over the half-group of entoderm cells and form a larva that is complete on the surface.

The final larva is abnormal in usually having only 4 ribs instead of 8 and 3 pouches instead of 4.

A second series of experiments seems to throw much light upon the influence of protoplasm versus nucleus in the causation of such imperfect development.

When a piece of the protoplasm of an entire egg is cut off, the egg, deprived of some protoplasm but with it nucleus intact, as far as known, develops into a larva that may be deficient in just the same way as is a larva reared from one of the isolated cells.

In another paper[7] Morgan finds the shaking method will not succeed with the blastulæ of Sphærechinus as they die when shaken. In Echinus, however, both blastulæ and gastrulæ may be shaken into pieces that will live.

[6] Idem, Oct. 25.95, pps. 444–447.

[7] Idem, pps. 257–266.

When pieces of the wall of the Echinus blastula are broken off they may form little blastulæ again and these may gastrulate. When these little blastulæ invaginate they tend to form more entoderm cells, in proportion to the entire number, than is the case in the normal blastula.

In Sphærechinus the normal blastula has about 500 cells and tends to invaginate about 50 ; in Echinus about the *same fraction of the whole* is invaginated, for of about 1000 cells about 100 go in to form the entoderm.

When young gastrulæ are shaken they may form abnormal larvæ owing, apparently, to changes in the mesoderm inducing abnormal skeletal growths and corresponding abnormal arms.

Pieces shaken out of the wall of a gastrula will not form into a blastula nor into a gastrula.

Likewise the entoderm when shaken out does not develop. Yet a gastrula that has had its entoderm removed by shaking will continue to grow and form a normal skeleton and arms.

A paper[8] on cross fertilization and the fertilization of non-nucleated pieces of eggs also by MORGAN goes over part of the ground of Boveri's remarkable work.

It is shown that small pieces of eggs of *Echinus miliaris* may be fertilized and develop as far as to the 16 cell stage. As the number of chromosomes in such cleaving masses is, in each nucleus, half the normal number it is inferred that such cleaving masses are the results of the entrance of one spermatozoa into a non-nucleated piece of an egg.

In attempting to cross fertilize pieces of eggs of Sphærechinus with sperm of Echinus it was found that the sperm entered the pieces only in few cases ; there is the same difficulty in crossing pieces of eggs as in crossing the whole egg with foreign sperm. The reverse is also the case; sperm of Sphærechinus will not readily enter pieces of eggs of Echinus.

It is, therefore not surprising that no larvæ were found that could be traced to non-nucleated pieces of eggs fertilized by a sperm of another species, which is the great desideratum in attempting to repeat Boveri's work.

When the whole eggs of Sphærechinus are fertilized by sperm of Echinus bastards result that are very variable and not all exact middle states between the larvæ of these two species. When the converse cross is attempted the larvæ are " for the most part very abnormal in appearance."

When the eggs of Sphærechinus are crossed with the sperm of Strongylocentratus the larva is very variable and not an intermediate form.

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[8] Idem, pps. 268–280.

The converse bastards also show great variation in the skeleton.

Boveri[9] republishes, is an amplified form with many new illustrations, his remarkable work on the cross-fertilization of enucleated fragments of sea urchin eggs, translated in the American Naturalist March 1, 1893. After considering the opposing results obtained by Morgan and by Seeliger the author still maintains that he has shown that a larva may be obtained from a piece of an egg without any nucleus and sperm of another species and that such a larva has none of the maternal characters but only those of the male parent, thus showing that the nucleus may transmit characters but that egg cytoplasm alone cannot do so.

The evidence for his conclusions is, however, of an inferential nature and a cautious jury may well hesitate before convicting Boveri of having deprived the cytoplasm of its share in the affairs of heredity.

The evidence as he now presents it seems to be about as follows.

1. When at Naples in 1889 he shook a lot of sea urchin eggs, *Echinus microtuberculatus* in a testtube many were broken into pieces of various sizes, with or without nuclei; when this collection was treated with sperm of the same species larvæ of all sizes down to $\frac{1}{20}$ of the normal were found.

2. When pieces that contain no nucleus, as far as could be seen under the microscope, were isolated and fertilized with sperm of the same species they developed into dwarf larvæ.

3. When the normal eggs of *Sphrœrchinus granularis* are treated with the sperm of *Echinus microtuberculatus* some few bastards result. In Boveri's original experiment all these bastards were half way between the larvæ of the parent species, both in external form and in the skeleton, which were very different in each pure larvæ form.

4. When the eggs of *E. microtuberculatus* are shaken and treated with sperm of the same species the larvæ present many abnormalities and some may have characters resembling those of another species.

5. When shaken eggs of *S. granularis* are treated with sperm of *E. microtuberculatus* large and small larvæ are formed; some few of the small ones, only a very few, 10 or 12 in all, were entirely of the Echinus or father type.

6. It was observed that the nuclei in any given area of a larva formed from a nonnucleated piece of Echinus egg and the sperm of the same species were, *on the average*, smaller than the nuclei in the corresponding area of a smaller larva formed from a nucleated piece.

7. The above few bastard larvæ of pure Echinus type had, on the average, smaller nuclei than similar larvæ of type intermediate between the two crossed parent.

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[9] Idem, Oct. 22, 1895, pps. 394--441.

The author maintains that the few dwarf bastards that were like the male parent came from nonnucleated pieces of Sphærechinus penetrated by a sperm of Echinus. This, however, is an indirect result of all the above facts, It should also be borne in mind that Morgan, as cited above, was not successful in obtaining a cross fertilization of enucleated fragments and that both Morgan and Seeliger[10] find the bastards between Sphærechinus and Echinus so variable that Boveri's experiment in which they appeared as exact intermediate forms seem an exception and hence may be withdrawn from the evidence.

HANS DRIESCH starting from the standpoint that it has been proved that isolated cleavage cells may produce an entire organism seeks to find where the limits of this power appear in the subsequent stages of development.

He cut blastulæ of Sphærechinus into pieces, chopping at random with scissors in a dish full of gastrulæ. When isolated the larger pieces formed gastrulæ or later larvæ, in most cases.

When the gastrulæ of the starfish, *Asterias glacialis* were cut in the same way some lost the inner end of the gastric invagination together with much ectoderm. After healing over the wound the new end of the gastric invagination enlarged and sprouted out the two cœlomic pouches that would have, normally, been formed from the part that was cut away: the power to form cœlemic pouches was thus vicariously assumed by a part that would normally have produced part of the definitive digestive tract. Such larvæ go on to form a normally three chambered digestive tract from what would, normally, have formed but part of the whole.

The author concludes that the powers of the ectoderm or of the ento. derm cells are as yet not restricted as to what organs or parts they may form in their proper germ layer.

When larvæ with the mesenchyme were cut and a piece with only ectodermal cells was isolated in 53 cut of 99 cases no gastrulation took place but only a healing of the wound though life and activity might last for a week.

In a few cases when the digestive tube was removed from such larvæ it did not grow but died after a few days. In 19 cases where the end of the gastric invagination was removed after it had enlarged and sprouted out the cœlemic pouches 17 did not form new cœlemic pouches. In like manner when a cut happened to remove the skeleton of one side it was not formed again.

We thus soon come to a state in which the primitive tendency of cells to replace others in organ formation seems lost.

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[10] See AMERICAN NATURALIST, March, 1895.

In all these cases the author will not grant that any *true regeneration* of lost parts takes place.

In the course of his discussion of the influence of yolk upon gastrulation PAUL SAMASSA[11] states that he has performed the following experiments upon frogs' eggs.

The eggs were injured, without breaking the egg membrane, by an induction shock applied from needle points to certain cells or groups of cells in the eight-cell stage of cleavage.

When the four vegetative cells are injured there may result a cell mass lying in two layers upon a mass of yolk and evidently representing, as seen in actions, a normal gastrula minus parts of its ectodermal structures. On the other hand injury to the animal cells results in a mass of cells lying near an inert mass of matter and possibly representing only entodermal cells.

These facts are interpreted as meaning that the animal or the vegetative cells may continue their development for some time independently of life, or at least of the perfect state, of the other cells.

These eggs die without reforming the injured parts by postgeneration.

In an extensive theoretical part of the paper the author places himself in the main, on the side of Hertwig as believing in epigenesis rather than in any form of preformation.

The last paper that we can notice here is that of AMEDEO HERLIZKA[12] who succeeded in tying a thread about the eggs of *Triton cristatus* in such a way as to completely separate the first two cleavage cells.

Hertwig compressed eggs by this method so that they formed hourglass shaped masses a single embryo finally resulted.

But in these experiments where the egg is separated into two distinct halves each develops by itself. From one half of the egg there results an embryo that may live to have a medullary tube and a notochord. This embryo was formed by a process of cleavage like that of an entire egg and not like the cleavage of half an egg.

The author holds that neither Weismann's nor any other ideas of preformation will suffice to explain such phenomena, but that we must accept some form of epigenesis.

He thinks that each of the first two cells is *totipotent* and normally makes half of the embryo when in the normal union with its fellow because of some *inhibition* of its power to produce the whole. In a case of postgeneration we might suppose that this inhibition was removed for a while and then resumed.

[11] Idem, Oct. 22, 1895.

[12] Idem, pps. 352--366.